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Research Article

Distribution and substrate preference of the invasive clam *Corbicula fluminea* in the river Rhine in the region of Basel (Switzerland, Germany, France)

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Abstract. The Asiatic clam *Corbicula fluminea* invaded the river Rhine in the Netherlands and Germany in the 1990s. It was first recorded in Switzerland (Basel) in 1995. We examined the distribution of the clam at 76 sites along the bank of the river Rhine, in three first order tributaries (Wiese, Birs, Ergolz) and in the Canal de Huningue in the region of Basel (Switzerland, Germany and France) in 2003. *C. fluminea* was found in the river Rhine and in the Canal de Huningue, which obtains water from the river Rhine. *C. fluminea* was recorded 22 km upstream of Basel, but not any further. This indicates a mean upstream spread of 2.4 km per year. It had not yet colonized any of the first order tributaries examined. The clam was most abundant on fine-grained substrates (sand) with slowly flowing, shallow water. This finding was confirmed by a substrate choice experiment in the river Rhine. Our results show that the spread of *C. fluminea* in the river Rhine does not stop where cargo shipping ends. Passive dispersal by waterfowl and recreational boating may facilitate further upstream spread. *C. fluminea* might be less successful in colonizing rivers with rapid current such as first order tributaries. These are assumed to serve as refuges for native molluscs.

Key words. Asiatic clam; invasive species; range expansion; substrate choice.

Introduction

The spread of invasive species is generally recognized as one of the major threats to biodiversity (Meffe and Carroll, 1997). The effects of non-indigenous plants and animals on natural communities in rivers and lakes are well documented (Josefsson, 1999; Westman and Savolainen, 2001; Dönni and Freyhof, 2002). For example, introduced mollusc species may reduce or even eliminate native mollusc fauna by competition (Byers, 2000; Strzelec, 2000; Cowie, 2002; Maronas et al., 2003). In other cases, however, introduced molluscs coexist with native mollusc species (Pointier and David, 2004).

The influence of the bivalve *Corbicula fluminea* (O. F. Müller, 1774) on indigenous species is inconsistent. It can coexist with other bivalves at some sites (Savannah River, South Carolina; Leff et al., 1990; Ohio River, Ohio; Miller and Payne, 1998), but can also severely affect native mollusc assemblages at other places (*C. fluminea manilensis* Philippi, 1844, Altamaha River, Georgia; Gardner et al., 1976; sedimentation basin at a nuclear power plant, South Carolina; Boozer and Mirkes, 1979; St. Johns River, Florida; Belanger et al., 1990).

C. fluminea, originating from Southeast Asia, began to expand in the 20th century. It is now widespread in rivers of North and South America as well as in Europe. In the river Rhine, *C. fluminea* was first recorded in the Nether-

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lands in 1985 (Glöer and Meier-Brook, 1998). Since the clam was found in the Lower Rhine, it has spread rapidly upstream most probably with cargo ships. Six years later, the species was found near Karlsruhe (Germany), 675 km upstream of Rotterdam, and in 1995 *C. fluminea* was first reported in Switzerland near Basel, 865 km from Rotterdam (Rey and Ortlepp, 2002). Den Hartog et al. (1992) suspected that a spill of toxic waste (Sandoz accident) near Basel in 1986, affecting the whole river over hundreds of kilometres, contributed to the clams' success because most of the invertebrates were killed and, as a consequence, their niches were unoccupied. However, independent of this accident, molluscan diversity of the river Rhine declined strongly in the past 150 years because of huge river corrections, industrial pollution, organic sewage and other invading species (Kinzelbach, 1972). Compared to the North American diversity of molluscs with 300 species of native unionid bivalves, the river Rhine appears to be species-poor with 22 bivalve and 33 gastropod species (including newly introduced species; IKRS, 2002; Panama City Fish and Wildlife Service, 2004).

In Europe, two *Corbicula* species are distinguished (*Corbicula fluminea* and *Corbicula fluminalis*, O. F. Müller 1774). To date, it is yet unclear whether more *Corbicula* species occur in Europe. A recent morphometric analysis showed that two distinguishable morphotypes with few intermediates coexist in the river Rhine (Pfenninger et al., 2002). DNA-analysis resulted in three highly distinctive genotypes without intermediates. Interestingly, the morphological traits seem to be unreliable, since both morphotypes showed all genotypes. For that reason, Pfenninger et al. (2002) suggested to refer to the *Corbicula*-complex. In our study, 98.7% of the clams belonged to the morphotype of *C. fluminea*. It is therefore likely that we are dealing with only one species of *Corbicula*.

It was hypothesized that the spread of *C. fluminea* would stop in the river Rhine where cargo shipping ends (i.e. in Rheinfelden, 20 km upstream of Basel). We tested this hypothesis by examining the current distribution of *C. fluminea* in the river Rhine and its tributaries in the region of Basel. We also assessed seasonal changes in the size structure of a *C. fluminea* population in the Rhine. To test whether the substrate preference of *C. fluminea* observed in the river Rhine results from active choice, we conducted a controlled choice experiment in which three different types of substrates were offered to clams. Knowledge on the rate of spread and the substrate preference of invasive clams could be helpful in managing river structures to suppress spreading of the clam.

Materials and methods

Field survey

We examined the distribution of *C. fluminea* at 76 sites along the bank of the river Rhine (mean discharge: 1,032 m^3/s), in three first order tributaries (Wiese, 11.3 m^3/s; Birs, 15.2 m^3/s; Ergolz, 1.9 m^3/s) and in the Canal de Huningue (12.0 m^3/s) in the region of Basel. Substrate of these tributaries was sampled qualitatively. Bottom samples were taken along the river at distances ranging from 200 m to 1 km in spring, summer and autumn 2003. Apart from the minimum distance of 200 m, sampling sites were chosen depending on accessibility. For the river Rhine, we focused on the bank in the city of Basel, the sections near first order tributary estuaries and the furthest upstream sites where *C. fluminea* was known to occur (near Rheinfelden in 2001; C. Oberer, pers. comm.).

At each sampling site ecological variables were recorded following Baur and Ringeis (2002): altitude (range 230–280 m a.s.l.), width of the river, water depth at the sampling site (mean of three measurements), and water current at the surface (classified into three groups and measured with the use of a table tennis ball (mean of five measurements): (0) standing water, (1) slow, ≤0.3 m/s, and (2) fast >0.3 m/s). Additionally, the type of substrate (silt <0.063 mm; sand: 0.063–2.0 mm; gravel: 2.1–63.0 mm; stones 63.1–200 mm; boulders and bedrock >200 mm; DIN 4022), light exposure of the habitat (assigned to three classes: (1) shady, (2) lightly sun-exposed, and (3) sun-exposed), and the type of the habitat adjacent to the river was assessed. We also recorded the type of riverbank.

The presence of *C. fluminea* was recorded as follows: (0) absent, (1) empty shells present, and (2) living individuals (>3 mm in shell length) present. Where living clams were found, their abundance was estimated according to Rey and Ortlepp (2002): I (1–9 individuals/m^2), II (10–20 ind./m^2), III (21–50 ind./m^2), IV (51–200 ind./m^2), V (201–500 ind./m^2), VI (501–1000 ind./m^2) and VII (>1,000 ind./m^2). For abundance estimates, substrate including clams from an area of 1 m^2 was sampled with a D-framed net.

We also examined the spatial distribution of *C. fluminea* in a cross-section through the river Altrhein (47°38′ N, 7°34′ E), a remnant of the former river Rhine (mean discharge 30 m^3/s), 4 km north of Basel. Bottom samples were taken along a transect of 150 m from the French to the German bank at depths ranging from 10 to 150 cm. Depth and type of substrate were recorded. The deepest part (37 m wide) could not be examined due to high water current.

To examine seasonal changes in the size structure of a *C. fluminea* population, clams were collected at intervals of approximately 6 weeks from spring to autumn 2003 (10 March, 21 April, 29 May, 10 July, 21 August, 2 October) at the same site in the river Altrhein. Samples were obtained as described above. To obtain juveniles, samples of 1 L bottom substrate were dried at 80 °C for 24 h, put through sieves with mesh sizes of 6.3, 2.0, 1.0 and 0.2 mm and later examined under a binocular microscope. Shell length and height of each clam were measured with a caliper to the nearest 0.1 mm. For clams <4.0 mm, a binocular microscope with stage micrometre was used. Water temperature was recorded at each sampling occasion. Data on the water chemistry of the river Rhine were obtained from the station Weil am Rhein (Germany) near Basel (AUE, 2003).

Substrate preference experiment

To examine the substrate preference of *C. fluminea*, we conducted a field experiment in the river Altrhein. The experimental design followed Belanger et al. (1985) and Olabarria et al. (2002). Four replicates with a total of 576 clams were run between July and October 2003. A replicate consisted of six plastic containers (30 cm in diameter, 15 cm deep), each of them subdivided with plastic walls into three sectors of equal size. Three containers were filled with three different types of substrate (T1–T3) for testing the clams' preference and three containers were filled with the same type of substrate in all sectors to examine the distribution of individuals by chance (T4–T6; Fig. 1). The following substrates were chosen: sand (A, 0.2–2 mm, obtained from the river Altrhein, organic matter content (OMC) = 3.7 %), fine gravel with sand (B, 1–3 mm, from the river Rhine near Huningue, OMC = 1.6 %), and gravel (C, 2–63 mm, from the river Rhine near Huningue, OMC = 3.8 %). It was hypothesized that the animals will move to the sector containing the most preferred substrate. Before the experiment, the substrates were dried at 80 °C for 24 h to remove benthic organisms. Plastic containers were positioned in the river Altrhein in such a way that the substrate surface was situated at a depth of 13–18 cm. Individuals of *C. fluminea* (>12 mm in shell length) were collected at the experimental site immediately before the tests. For each container 24 clams were randomly assigned to three groups of eight individuals each. The 24 clams per container correspond to a density of 340 individuals/m^2. The clams of each group were labelled individually using a water resistant paint marker. The clams were placed group-wise on the line separating two sectors (Fig. 1). The sector opposed to the current was referred to position I, the other sectors clockwise to position II and III (the current was parallel to the wall separating sector II and III). The same procedure was used for the three containers with a single substrate. An experimental trial lasted for 2 h. After 1 h, 70–80 % of the clams were already buried in the substrate, confirming the findings of Belanger et al. (1985). At the end of each trial we recorded the position of each clam. Preliminary studies, in which clams were placed in the centre of each sector, revealed immediate vertical movements. Within a few minutes most clams started to investigate the environment with their feet. Once having moved to the preferred sector the clams began to bury.

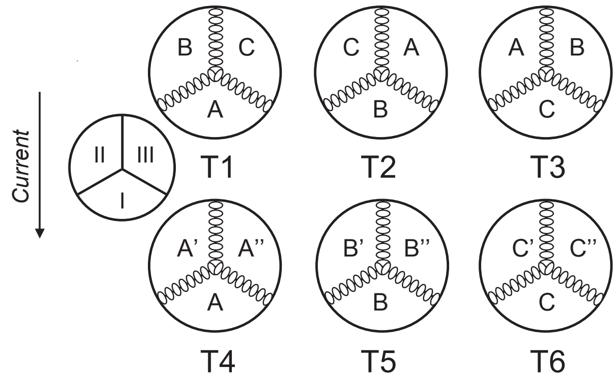

Figure 1. Experimental design with the treatments T1–T6 to test the substrate preference of *Corbicula fluminea*. Containers were subdivided into three sectors of equal size. Each sector contained a substrate: A refers to sand, B to fine gravel with sand, and C to gravel. Dots on the separating walls represent the clams' starting positions. The arrow indicates the water current.

Statistical analyses

Data analysis was performed using StatView (Version 5.0, Abacus Concepts, 1998). The frequency of occurrence of *C. fluminea* in relation to different substrate types and environmental variables was analysed using contingency tables. The effect of single environmental variables on the presence/absence of *C. fluminea* was examined using a logistic regression model. In the field experiment, deviations of the clams' substrate choice from a uniform distribution (no choice) were analysed using contingency tables.

Results

Field survey

Specimens of *C. fluminea* were exclusively found in the river Rhine, in the Canal de Huningue, and in streams connected with the Canal de Huningue (Fig. 2). The Asiatic clam could not be found in any of the first order tributaries Wiese, Birs and Ergolz. Living specimens of *C. fluminea* were recorded at 22 of 76 investigated sites (28.9 %), empty shells at a further 8 sites (10.5 %). In the river Rhine, *C. fluminea* has spread 22 km upstream of Basel as indicated by two living individuals (both measuring 15 mm in shell length) and two empty shells. At other potentially suitable sites further upstream, *C. fluminea* was not recorded in 2003.

In the river Rhine, the local density of *C. fluminea* decreased towards the current edge of distribution. In the river Altrhein (7 km downstream of Basel), 200–600 clams/m^2 were recorded. In Basel, the density of *C. fluminea* varied from 5–200 individuals/m^2 and at localities situated upstream of Basel from 1–20 individuals/m^2. In the Canal de Huningue, densities of 10–50 individuals/m^2 were recorded.

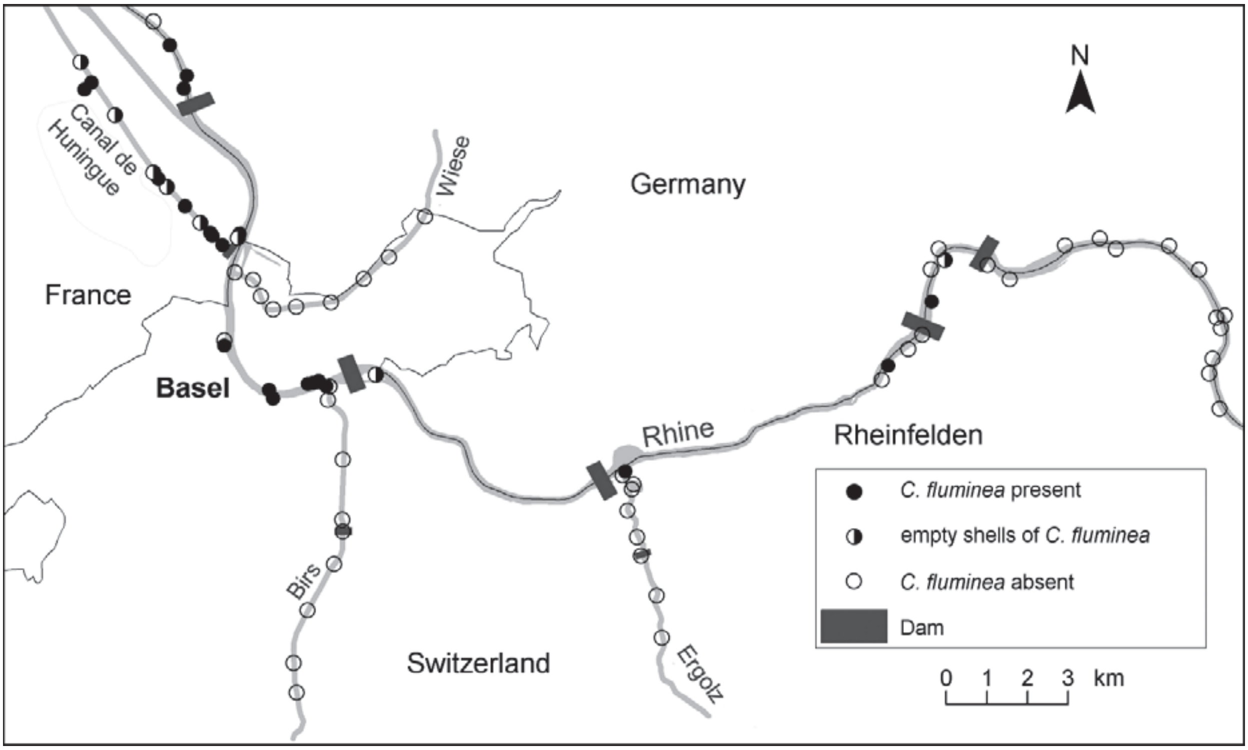

Figure 2. Distribution of *Corbicula fluminea* in the surroundings of Basel in 2003.

The occurrence of *C. fluminea* was influenced by the type of substrate (χ^2 = 19.92, *df* = 4, *P* = 0.0005). The clam was most frequently found on fine grained substrates such as silt (33.3 %), sand (33.3 %) and fine gravel (30.0 %). Hard substrates such as bedrock and boulders were never occupied by the clam, except for juveniles of up to 3 mm shell length, which were attached to large stones and other adult clams. Water current also affected the occurrence of *C. fluminea* (χ^2 = 16.38, *df* = 3, *P* = 0.0009). Living clams were exclusively found in slowly running and standing waters. No effect of light exposure, vegetation of the bank, water depth at sampling site or river width of the site on the presence of *C. fluminea* was found (logistic regression, in each case $P > 0.2$).

The transect sampling across the river Altrhein revealed that *C. fluminea* was most abundant (up to 600 clams/m^2) on sandy substrates near the banks of the river. The abundance decreased with increasing water current towards the middle of the channel. No *C. fluminea* was found at places where the substrate consisted of stones.

The size distribution of *C. fluminea* in the river Altrhein indicated the presence of a well-established population (Fig. 3). The size distribution recorded on 10 March 2003 showed four peaks which may refer to four cohorts (1–4). Cohort 1 with a median shell length of 19 mm was the oldest, followed by cohort 2 (peak at a shell length of 14 mm), cohort 3 (9 mm) and cohort 4 (2.2 mm). In April cohort 4 was only represented by empty valves and was therefore not considered in the size distribution. In August, a new cohort (5) appeared with a peak at a shell length of 4 mm.

In all cohorts, the growth rate was highest between May and October (Table 1), most probably favoured by an increased water temperature (10 March: 7 °C; 21 April: 12 °C; 29 May: 15 °C; 10 July: 22 °C; 21 August: 24 °C; 02 October: 17 °C) and food availability in that period. However, the abundance of plant nutrients in 2003 did not differ from the 10-year mean value (Table 2).

Substrate choice experiment

In the substrate choice tests, clams did not bury in equal frequencies in sectors with different substrates (T1–T3; χ^2 = 14.68, *df* = 1, *P* = 0.0006; Table 3). The clams moved most frequently into sectors containing sand (41.7 %) and less frequently into sectors containing fine gravel with sand (35.0 %) or gravel only (23.3 %). Thus, *C. fluminea* showed a preference for fine substrates. The position of the different substrate types in relation to the water current did not influence the preference of the clams (χ^2= 2.81, *df* = 1, *P* = 0.25). In containers with a single substrate (T4–T6), clams buried in equal frequencies in all sectors (χ^2 = 0.53, *df* = 1, *P* = 0.77). Water current slightly influenced the clams' choice of the sector in containers with a single substrate (T4–T6; χ^2= 6.79, *df* = 1, *P* = 0.034; Table 3). Most clams showed a positive rheotaxis.

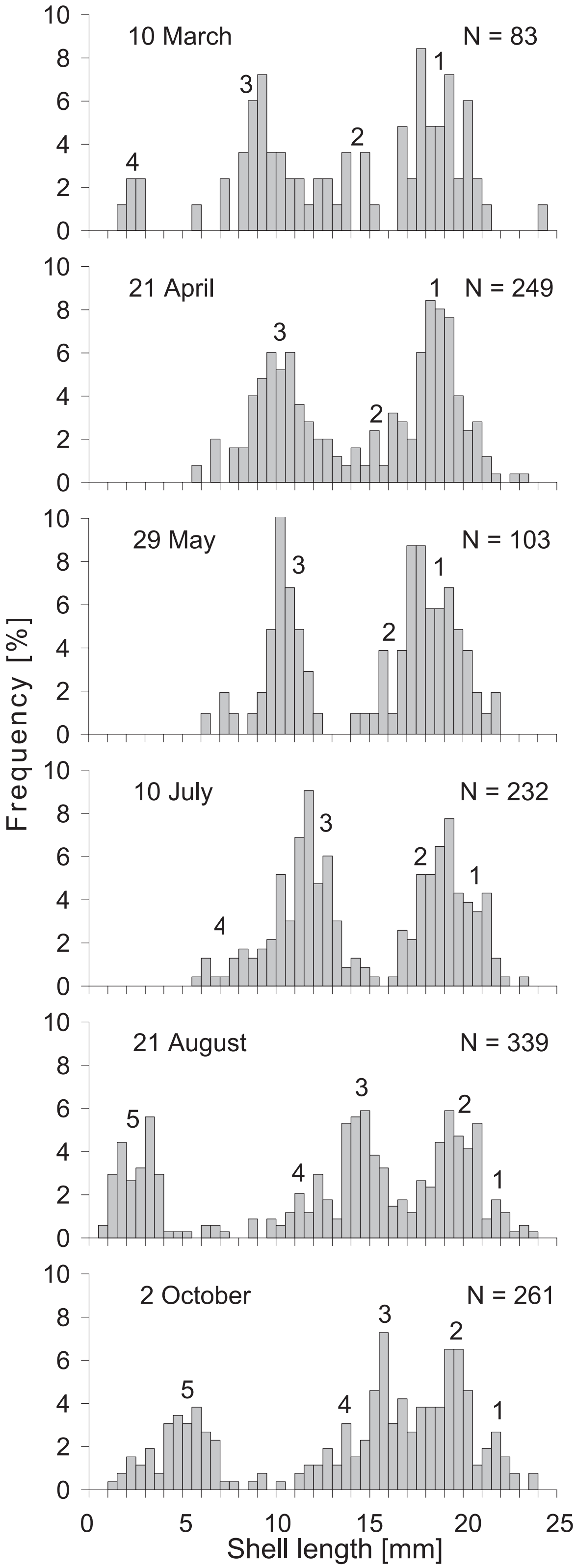

Figure 3. Seasonal changes in the size distribution of *Corbicula fluminea* in the river Altrhein near Basel between 10 March and 2 October 2003. The numbers 1–5 on the top of the bars indicate the possible cohorts; N refers to the numbers of clams measured, which were grouped in size classes of 0.5 mm.

However, the effect of the substrate type was much stronger than the effect of the water current (randomised positions of substrate types in T1–T3).

Discussion

C. fluminea arrived in Basel (Switzerland) in 1995 (Rey and Ortlepp, 2002). In 1997, *C. fluminea* was found near Augst, 11 km upstream of Basel, and in 2001 near Rheinfelden, 20 km upstream of Basel (C. Oberer, unpubl. data). In our survey, *C. fluminea* was recorded 2 km upstream of Rheinfelden in 2003, indicating a mean upstream spread of 2.4 km per year in the last 9 years. Compared with the annual dispersal distance since the clam entered the river Rhine in 1985, this is a low rate of spread (Glöer and Meier-Brook, 1998). It is commonly assumed that the clam was introduced and spread by ballast water of cargo ships (Morton, 1986) and that the larvae colonize downstream habitats by the water currents independently of shipping. Since cargo ships in the region of Basel rarely need ballast water, the clams must have other means of dispersal. We found one-year old *C. fluminea* upstream of the barrage of Rheinfelden where no cargo shipping occurs. From Rheinfelden upstream to the outlet of Lake Constance, *C. fluminea* does not yet occur (personal communication from three fishery inspectors: T. Stucki, K. Balsiger, J. Walter, 2003). However, new occurrences of *C. fluminea* were reported from Lake Constance in August 2003 (Werner and Mörtl, 2004) and from Lake Neuchâtel in November 2003 (Rey, unpublished data), and most recently, in Lake Morat in July 2005 (Fasel, 2005). These new occurrences may result from independent non-intentional introductions.

In a protected area of the Savannah River (South Carolina), waterfowl has been suggested to displace *C. fluminea* at least 1.2 km per year (Voelz et al., 1998). Juvenile *C. fluminea* use their mucous secretions (Prezant and Chalermwat, 1984; Dubois, 1995; Schmidlin, 2004) to stick to ducks' feet and to fishes (Brancotte and Vincent, 2002), and thus might be transported over large physical barriers such as dams of hydro-electrical power plants. Adult clams can also attach to macrophytes by valve closure or getting stuck between the filaments/threads of algae (*Elodea* sp., *Cladophora* sp.), when the plants were pulled out of the water (H. Durrer, pers. comm.; Schmidlin, 2004). Accidental transportation of *C. fluminea*, sticking on macrophytes (e.g. by recreational boating) may further contribute to its spread.

C. fluminea is used as fish bait by fishermen (Cazzaniga and Perez, 1999; Brancotte and Vincent, 2002) and sold as aquarium or pond accessory in pet shops and garden centres (Werner and Mörtl, 2004). When cleaning an aquarium, the clam might be released into streams or lakes, as has been done with the gastropods *Physella* cf.

Table 1. Mean shell length (SL; mm) and growth rate (Δ SL; mm/30 days) of each cohort in the river Altrhein in 2003. The age and the year of spawning were estimated (a = first spawning; b = second spawning) based on the shell length in October 2003.

Date		Cohort				
		1	2	3	4	5
10 March	SL	19.0	13.75	8.5	2.25	
	Δ SL	*0.36*	*1.25*	*0.54*	-	
21 April	SL	19.5	15.5	9.25	-	
	Δ SL	*0.00*	*0.79*	*0.00*	-	
29 May	SL	19.5	16.5	9.25	-	
	Δ SL	*1.07*	*1.07*	*1.96*	*1.41**	
10 July	SL	21.0	17.0	12.0	8.0	
	Δ SL	*0.71*	*1.43*	*2.50*	*2.32*	
21 August	SL	22.0	19.0	15.5	11.25	4.0
	Δ SL	*0.18*	*0.18*	*0.71*	*1.25*	*1.25*
2 October	SL	22.25	19.25	16.5	13.0	5.75
10 March – 2 Oct.	absolute SL growth	3.25	5.5	8.0	10.75	1.75
	Δ SL	*0.47*	*0.80*	*1.17*	*1.57*	
Age; year of spawning		3+; 2000	2+; 2001	1+; 2002a	1–; 2002b	1–; 2003

* from March to July.

Table 2. Water chemistry data of the river Rhine at the station Weil am Rhein (Germany). Mean values and ranges were determined from fortnightly analyses. DOC: Dissolved Organic Carbon; SM: Suspended Matter (AUE, 2003; IKRS, 2005).

Parameters	2003		1995-2004	
	Mean	Range	Mean	Range
Oxygen (mg/l)	10.11	7.6–13.3	10.65	7.6–13.8
pH*	8.00	7.55–8.41	8.14	7.9–8.4
Temperature (°C)	14.0	3.5–26.7	12.6	3.8–25.3
Conductivity (µS/cm)	363.0	287.8–442.4	355.6	290.0–445
Discharge (m^3/s)	804.4	375–2125	1099.2	457–3216
DOC (mg/l)	2.18	1.57–3.52	2.07	1.1–3.8
SM (mg/l)	6.8	1.4–19.6	15.9	1–834.3
NH_4^+ (mg/l)	0.069	0.0338–0.113	0.071	0.02–0.226
NO_3^- (mg/l)	1.33	0.918–1.893	1.48	0.92–2.29
PO_4^{3-} (mg/l)	0.043	0.020–0.126	0.045	0.01–0.141

*data not available from the years 1999–2002.

acuta and *Planorbella* spp. (Horsak et al., 2004). It is assumed that both non-intentional and deliberate introduction of *C. fluminea* are important factors increasing the spread of this species.

Of the ecological variables examined only substrate type and water current affected the occurrence of *C. fluminea*. However, because substrate type (grain size) is correlated with water current (Dudgeon, 1982), *C. fluminea* was most frequently found at sites with fine sediments and slow water current. Several hypothesis may explain the occurrence of *C. fluminea*. First, water current is an important factor in determining successful colonisation because it also determines food supply. The downstream increase of phytoplankton depends on flow duration, generation time of phytoplankton and increasing nutrient concentration (Yang et al., 1997). The outlet of Lake Constance and the numerous reservoirs adjacent to dams may provide sufficient phytoplankton for *C. flu-*

minea and other organisms living in the Rhine. In the turbulent tributaries examined, the productivity of seston, foremost micro-algae, could be limited and therefore not allow *C. fluminea* to reproduce, even though the clam is able to pedal-feed (Hakenkamp and Palmer, 1999; Rajagopal et al., 2000; Mouthon, 2001a; 2001b).

Another hypothesis relates to the changing amount of water: Invasive clams may be sensitive to fluctuations in water height and current (periodic sediment turnover and transportation, falling dry; Rey et al., 2004). However, variation in water height and current are less pronounced in the river Rhine than in the tributaries examined. Furthermore, low water temperature has been suggested to limit the spread of *C. fluminea* (Schöll, 2000). In the rivers examined in the present study, the water temperature of the tributaries Birs and Ergolz is not lower than that of the river Rhine.

Table 3. Results of the substrate choice experiment. Figures indicate the number of *Corbicula fluminea* that chose a particular substrate type. Data of four replicates are pooled. Treatments are explained in Figure 1.

Treatment	Substrate		
	Sand (A)	Fine gravel with sand (B)	Gravel (C)
T1	31	37	25
T2	44	31	21
T3	43	31	20
T4	32/34/30[a]	–	–
T5	–	35/26/34[a]	–
T6	–	–	34/35/27[a]

[a] Corresponds to the number of clams found in the sectors X/X'/X'' in Figure 1.

Size distribution

In the population examined in the river Altrhein, we recorded slightly different size distributions compared with those found in the Upper Rhine near Mainz (Meister, 1997). The Altrhein population most probably contained 2- to 3-year-old clams in October 2003, while 4- to 5-year-old individuals were found near Mainz. Growth conditions in the Altrhein may be more similar to those of the river Saone in France (Mouthon, 2001a). Saone populations are characterised by a single annual reproduction period starting in May or June and ending in September or October. In our study, the spawning period most probably occurred in June and July because the first juveniles were recorded in August (cohort 5).

Substrate choice experiment

The results of our substrate choice experiment confirmed field observations and experimental evidence of Belanger et al. (1985), who found that *C. fluminea* prefers fine substrates, which contain more organic material (= potential food) than coarse ones (Dudgeon, 1982). It could be expected that the clam moves to the substrate which provides the most food. In our experiment gravel contained most the organic matter in the form of hard layers consisting of fine sediments. However, in this form organic matter is only separable at high temperatures (700 °C) and therefore cannot be used by *C. fluminea*.

Our choice experiment also showed that the direction of water current can influence clam behaviour in homogeneous substrates (containers T4–T6). A positive rheotaxic behaviour allows the clams to move upstream without hitchhiking. However, since the majority of adult clams are buried in the substrate, the effect of current direction might be small. Molluscan upstream movements are frequently explained by search for food or space, compensation of drift, avoidance of predation and by hydrodynamic and biomechanical effects (Huryn and Denny, 1997).

Effects on other species

C. fluminea could become a threat to other organisms, if it uses the same resources as other species. The most important resources to the clam are space and food. The favoured spatial resource, different types of fine substrate, is also used by unionids. Four species of unionids are known to occur in the region of Basel (Glöer and Meier-Brook, 1998). In 2000, only empty shells of the clams *Unio pictorum* (Linnaeus, 1758) and *Unio tumidus* (Philipsson, 1788) were found (Rey and Ortlepp, 2002). *C. fluminea* may compete with filter-feeders (other bivalves) and also with benthic consumers of organic matter.

Indeed, a preliminary study indicated that the molluscan assemblage experienced profound changes in the river Rhine near Basel between 1994 and 2003 (Schmidlin, 2004). In 1994, *C. fluminea* did not yet occur at the two sites examined in Basel (Baur and Ringeis, 2002). Nine years later, however, *C. fluminea* was together with the gastropod *Ancylus fluviatilis* (O. F. Müller, 1774) the most abundant mollusc at both sites and gastropod diversity has decreased. This decrease in species richness could partly be a result of competition with *C. fluminea* for space and food (Schmidlin, 2004). The recent invasion of other species such as the polychaet *Hypania invalida* (Grube, 1860) and the amphipods *Chelicorophium curvispinum* (Sars, 1895) and *Dikerogammarus villosus* (Sovinsky, 1874) put additional pressure on native communities (Rey and Ortlepp, 2002). However, experimental studies are needed to determine the impact of *C. fluminea* on native molluscan assemblages.

Conclusions

Our data show that the current distribution of *C. fluminea* in the river Rhine does not stop where cargo shipping ends. But the expansion of the clam is slow in comparison to the former spread in the river Rhine. Natural upstream movements of bivalves are hardly known. However, passive dispersal by waterfowl and recreational boating may facilitate further upstream spread of *C. fluminea* in the river Rhine. The substrate choice experiment showed that *C. fluminea* prefers fine grained sediments. *C. fluminea* seems to be less successful in colonizing rivers with rapid current such as first order tributaries, in which the preferred substrate is less abundant. These tributaries may serve as refuges for native molluscs. Our study documents the initial phase of the invasion of *C. fluminea* in Switzerland. Most probably, this invasive species will further expand and colonize other rivers and lakes.

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